DISCUSSION

Comment — Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (^{137}Cs)[1]

Jixiang He and Donald J. Stewart

Rowan and Rasmussen (1996) reported that mature fish have two- to four-fold higher activity than immature fish, so the former do not follow the rule that specific respiration rate decreases with increasing body mass. Their modeling results contradict Koch and Wieser's (1983) experimental results in which gonadal synthesis drastically reduced swimming activity. We find that Rowan and Rasmussen's results may come from an error in their model development. To make the point clear, we repeat Rowan and Rasmussen's theoretical analyses (using their equation numbers) as follows:

$$(2) \qquad W_t = W_0 e^{Gt}$$

where W is body mass (g), t is time, and G is the specific growth rate ($g \cdot g^{-1} \cdot t^{-1}$). Notice that $G = (\log_e(W_t) - \log_e(W_0))/t$, and it does not include reproduction.

$$(3) \qquad dQ/dt = \alpha[^{137}Cs_f]CW_t - (E + D)Q$$

where Q is ^{137}Cs burden (Bq), D is the specific radioactive decay of ^{137}Cs ($Bq \cdot Bq^{-1} \cdot t^{-1}$), E is the elimination rate of ^{137}Cs ($Bq \cdot Bq^{-1} \cdot t^{-1}$), C is the specific rate of food consumption ($g \cdot g^{-1} \cdot t^{-1}$), $[^{137}Cs_f]$ is Cs concentration in food ($Bq \cdot g^{-1}$, in Rowan and Rasmussen's paper, they give $Bq \cdot kg^{-1}$), and α is the assimilation efficiency of ^{137}Cs. Combining eqs. 2 and 3 gives

$$(4) \qquad dQ/dt = \alpha[^{137}Cs_f]CW_0 e^{Gt} - (E + D)Q$$

Integrating eq. 4 gives

$$(5) \qquad Q_t = \frac{\alpha[^{137}Cs_f]CW_0(e^{Gt} - e^{-(E+D)t})}{(G + E + D)} + Q_0 e^{-(E+D)t}$$

In Rowan and Rasmussen's paper, the last term is incorrectly given in the numerator of the first term for both eqs. 5 and 6. We suspect that was a typographical error because their eq. 7 was mathematically correct but cannot be derived from their eqs. 5 and 6. However, that is not the main problem that we want to discuss here. For mature fish, Rowan and Rasmussen (1996) consider that "if spawning occurs during the period modelled, the ^{137}Cs lost in eggs and sperm (Q_g) should be subtracted." Therefore, they have

$$(6) \qquad Q_t = \frac{\alpha[^{137}Cs_f]CW_0(e^{Gt} - e^{-(E+D)t})}{(G + E + D)} + Q_0 e^{-(E+D)t} - Q_g$$

Finally, they solve for the specific rate of consumption as

$$(7) \qquad C = \frac{(Q_t - Q_0 e^{-(E+D)t} + Q_g)\,(G + E + D)}{\alpha[^{137}Cs_f]W_0(e^{Gt} - e^{-(E+D)t})}$$

The biological problem is the inconsistency between eqs. 2 and 6. The specific rate of growth (G) is calculated from the difference between somatic masses W_t and W_0. Thus, the ^{137}Cs consumption, assimilation, decay, and elimination in eqs. 2, 3, 4, and 5 do not account for any ^{137}Cs in eggs and sperm. For immature fish, the treatment in eqs. 6 and 7 does not have any effect on calculation of consumption because Q_g is zero. For mature fish, the specific rate of consumption (C) in eqs. 3, 4, and 5 is different from the "specific rate of consumption" in eqs. 6 and 7. If reproductive losses (Q_g) are to be subtracted during the calculation of consumption (eqs. 6 and 7), then reproduction should be included in eqs. 2–4. This inconsistent treatment of reproduction may fully explain discrepancies between their model results for mature fishes and those from more traditional energetics-modeling approaches.

According to eqs. 2–7, the specific rate of consumption might have been underestimated because the time scale in their study was 1 year. In eq. 5, $\alpha[^{137}Cs_f]CW_0 e^{Gt}$ is the ^{137}Cs assimilation at the end of a year, while $\alpha[^{137}Cs_f]CW_0 e^{-(E+D)t}$ is ^{137}Cs elimination and decay based on ^{137}Cs assimilation at the beginning of the year. It is clear that elimination and decay are underestimated when the time scale is a year rather than a shorter interval. Thus, eq. 7 might underestimate the specific consumption rate. Rowan and Rasmussen (1996) claimed that their method could be used on a weekly time scale, so the above problem would be solved. We agree that an exponential growth function can and should be used only for intervals much shorter than a year (Ricker 1975). We wonder whether or not individual variations in ^{137}Cs burden will confound the patterns suggested by eqs. 2–7 when short time scales are used.

The ^{137}Cs elimination rate (E; $Bq \cdot Bq^{-1} \cdot t^{-1}$) is an interesting term. According to Rowan and Rasmussen (1996), it is a negative

Received March 18, 1997. Accepted May 21, 1997.
J13922

J. He and D.J. Stewart. State University of New York, College of Environmental Science and Forestry, 302 Illick Hall, 1 Forestry Drive, Syracuse, NY 13210, U.S.A.

[1] Paper by D.J. Rowan and J.B. Rasmussen. 1996. Can. J. Fish Aquat. Sci. **53**: 734–745.

function of body mass and a positive function of temperature; therefore, it is similar functionally to respiration but different from excretion and egestion in fish bioenergetic models (Kitchell et al. 1977; Stewart et al. 1983). Johannes (1964) indicated that the rate of excretion of dissolved phosphorus per unit body mass decreases as body mass increases for marine animals. Edwards (1967) indicated that elimination of ^{65}Zn is a function of specific rate of respiration in plaice (*Pleuronectes platessa* L.). Can we reject the possibility that ^{137}Cs elimination is related to respiration? The primary objective of Rowan and Rasmussen's study was to develop a better method to estimate respiration related to activity. They use eqs. 2–7 to estimate consumption and then use fish bioenergetic models to calculate respiration. If we cannot reject the possibility that ^{137}Cs elimination is a function of respiration, then Rowan and Rasmussen's method will suffer from circularity.

Balancing a fish energy budget is sufficiently complex that no single approach can be totally free of bias. We apply fish bioenergetic models as comprehensive tools to improve our understanding of complex living systems and how they should be managed. We believe that application of multiple approaches to that larger goal can help to test alternative hypotheses and, ultimately, to minimize assumptions. Rowan and Rasmussen's (1996) study is important in that it introduces a new technique for evaluating in situ energetics of fishes. As applied, however, it suffers from the overly simplified exponential growth model and inconsistent treatment of reproduction. We look forward to further tests and applications of this new tool because, if it works, we all stand to benefit.

References

Edwards, R.R.C. 1967. Estimation of the respiratory rate of young plaice (*Pleuronectes platessa* L.) in natural conditions using zinc-65. Nature (London), **216**: 1335–1337.

Johannes, R.E. 1964. Phosphorus excretion and body size in marine animals: microzooplankton and nutrient regeneration. Science (Washington, D.C.), **146**: 923–924.

Kitchell, J.F., Stewart, D.J., and Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. **34**: 1922–1935.

Koch, F., and Wieser, W. 1983. Partitioning of energy in fish: can reduction of swimming activity compensate for the cost of production. J. Exp. Biol. **107**: 141–146.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Rowan, D.J., and Rasmussen, J.B. 1996. Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (^{137}Cs). Can. J. Fish. Aquat. Sci. **53**: 734–745.

Stewart, D.J., Weininger, D., Rottiers, D.V., and Edsall, T.A. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. **40**: 681–698.